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Short Communications

Chipping and wear patterns in extant primate and fossil hominin molars: ‘functional’ cusps are associated with extensive wear but low levels of fracture

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1. Introduction

Dental wear is the loss of dental hard tissues not caused by pathology or trauma. It consists of three main categories: attrition, abrasion, and erosion (Kaidonis, 2008; Grimoud et al., 2012; Burnett et al., 2013). Attrition and abrasion occur via teeth contacting one another or a foreign object, respectively, including during normal mastication. Erosion is caused by the effect of acids, from the consumption of acidic foods to intrinsic factors such as gastroesophageal reflux and rumination (Zero, 1996; Indriati and Buikstra, 2001; Deter, 2009; Ritter et al., 2009; Burnett et al., 2013; Hill, 2018), contra dental caries that are mediated by bacteria.

Another type of hard tissue loss can result from crown fracture, ranging from large cracks that expose the pulp to small surface chips. In the present study we focus on the latter. Chips can be caused by several factors including dietary items, facial trauma, malocclusion, environmental grit and cultural behavior (He and Swain, 2008; Constantino et al., 2010; Scott and Winn, 2011; Towle et al., 2017). Typically, the result entails crescent-shaped enamel removal from the outer rim of a crown (Sauther et al., 2002; Scott and Winn, 2011). Most other types of injury caused by trauma (e.g., craze lines or underlying soft tissue/bone damage) are generally not associated with dental tissue removal (Soukup, 2019), nor can they typically be studied in archaeological and fossil specimens due to taphonomic

processes. However, since crown chips are common and contribute to enamel/dentine removal, they are important to consider when comparing tooth wear patterns among species.

Both dental wear and chipping can provide information on diet and cultural practices (e.g., Tobias, 1980; Teaford, 1983; Janis, 1984; Ungar and Grine, 1991; Cuzzo and Sauther, 2006; Deter, 2009; Clement and Hillson, 2013; Morse et al., 2013). Moreover, they are interconnected, with differences in wear between individuals implicated in the likelihood of chipping presence, either due to enamel property changes as teeth wear, or because individuals with heavily worn teeth are usually older and have had more time for fractures to accumulate (Fannin et al., 2020). For example, enamel becomes thinner with age, which will alter the distribution of stresses; the mechanical properties of the enamel may also change (Park et al., 2008). However, it is not well understood which tooth crown locations (e.g., mesial, lingual, distal, or buccal) are most susceptible to chipping in different primate species, and if these patterns vary with progressive wear.

Variations in bite force and contact types have been linked to the evolution of enamel properties (Constantino et al., 2012; Cuy et al., 2002). In particular, maxillary lingual cusps often have thicker enamel than buccal surfaces, while the opposite is true in mandibular teeth (Kay, 1975; Molnar and Ward, 1977; Macho and Berner, 1993; Schwartz, 2000). Owing to these differences, lingual and buccal cusps are often compared in tooth wear and comparative morphology studies. This has led to the use of terminology such as ‘functional cusps’ for maxillary lingual and mandibular buccal cusps, and ‘non-functional cusps’ for their maxillary buccal and mandibular lingual

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counterparts (Khera et al., 1990; Schwartz, 2000). In this study, we use this terminology, even though both sides of the tooth are clearly functional.

Owing to the standard masticatory cycle how teeth occlude in primates, functional cusps tend to show more rapid localized wear (Macho and Berner, 1993; Schwartz, 2000; Kono, 2002). This process has been associated with higher stress in these areas, which may expose them to higher risk of chipping (Kay, 1975; Lucas et al., 2008; Thiery et al., 2017). Some researchers have suggested functional cusps may have evolved thicker enamel primarily in response to protection against fracture, not attrition (Grine, 2005). However, it is also suggested that functional cusps experience more shearing forces and non-functional molar cusps more crushing forces, related to movements in the masticatory cycle (Schwartz, 2000), to predispose the latter to more fractures. Human clinical studies support this latter hypothesis, as nonfunctional cusps often show higher fracture prevalence (Cavel et al., 1985; Eakle et al., 1986).

Therefore, although it is well known that wear is typically more substantial on molar surfaces with thicker enamel (i.e., functional cusps), it has not been explored if these same surfaces are also more prone to chipping — in this case among wild primates. Comparing these two types of tissue loss may provide further insight into the evolution of more robust functional cusps present in many primate species. In this study, molar wear and chipping patterns were compared in five fossil hominin, three extant ape, and three Cercopithecidae species, meaning a range of diets and dental characteristics are represented. Differences in chipping and wear patterns are then discussed in light of structural differences and functional implications, with a particular focus on comparing functional and nonfunctional sides. Based on limited human clinical evidence that chipping is more prevalent on nonfunctional cusps (Cavel et al., 1985; Eakle et al., 1986), we hypothesize that this same pattern will be observed in non-human primates as well.

2. Material and methods

The hominin specimens are attributed to *Paranthropus robustus*, *Homo naledi*, early *Homo*, *Australopithecus sediba*, and *Australopithecus africanus*; original specimens were studied in all instances. The extant primates are chimpanzees (*Pan troglodytes troglodytes*; Gordon et al., 2013), western lowland gorilla (*Gorilla gorilla gorilla*), Kloss's gibbons (*Hylobates klossii*), pig-tailed langurs (*Simias concolor*), hamadryas baboons (*Papio hamadryas*) and Japanese macaques (*Macaca fuscata*). Hominin samples are curated at the Ditsong National Museum of Natural History and University of the Witwatersrand. Primate samples are held at the Powell-Cotton Museum, UK (chimpanzees and western lowland gorillas), and Primate Research Institute, Kyoto University, Japan (Kloss's gibbons, pig-tailed langurs, hamadryas baboons and Japanese macaques). All of the latter were free ranging individuals (Guatelli-Steinberg and Skinner, 2000;

Lukacs, 2001; Kato et al., 2014; Asahara and Nishioka, 2017; Buck et al., 2018). The number of individuals (divided by sex) for the extant primate samples is listed in Supplementary Online Material (SOM) Table S1.

Although the terms 'functional' and 'nonfunctional' cusps are used, this study compared lingual and buccal sides of molars, with chipping and wear recorded regardless how much of the cusps remain, including molars with enamel rims. Only permanent molars free of postmortem damage were analyzed. Wear was scored following Scott (1979), who proposed dividing teeth into quadrants, with each given a score of 1–10. A value of 1 means a tooth is unworn or has negligible wear facets, while 10 describes complete loss of enamel. The two lingual and two buccal quadrants were combined, and the mean species value for side (buccal and lingual quadrants) calculated, allowing the two sides to be compared. This strategy allows for direct comparison of differences in wear between functional and nonfunctional cusps.

Data on chipping prevalence followed Towle et al. (2017), with additional species and data on chip location included. Teeth were observed macroscopically with a 10× hand lens to evaluate if a chip formed ante- or postmortem, i.e., if chip scars showed evidence of wear they were considered to have formed during life (Towle et al., 2017). The number and position of chips were recorded, with the latter comprising buccal, lingual, mesial, or distal occlusal edges. If the boundary between two sides (e.g., buccal and mesial) was not clear (i.e., if there is a gradual rounded corner between sides), a halfway point was approximated. If a tooth presented multiple chips, only the side with the greatest number was recorded. If multiple sides had the same number, the side with the largest chip was used. Finally, the average severity of wear score and chip prevalence were compared for buccal and lingual halves of both maxillary and mandibular molars. Overall chipping patterns (i.e., also including mesial and distal chipping) were also compared among species.

To assess the influence of increased wear on chipping patterns, the three largest extant primate samples (chimpanzee, Western lowland gorilla, and Japanese macaque), were divided into 'old' and 'young' individuals. This division was roughly 50:50 based on incisor wear (upper central incisor wear score: 'young': ≤5; 'old': ≥6 wear; Smith, 1984). Individuals with unerupted or missing upper central incisors were not included. The mean molar wear and standard deviations for each of these groups was calculated, along with chipping prevalence and position.

3. Results

Chipping prevalence was highly variable among species, from 5.76% in Kloss's gibbons, to 49.15% in *H. naledi* (Table 1). The extant primates showed greater differences in occlusal wear between buccal and lingual cusps in both upper and lower molars (Table 2). Of the hominins, *H. naledi* displays the greatest difference between

Table 1
Number of molars studied and number of chipped teeth (in brackets) for each species.

| Species | Common name | First molars | Second molars | Third molars | Total molars | Chipping prevalence (%) |
|-----------------------------------|-------------------------|--------------|---------------|--------------|--------------|-------------------------|
| <i>Pan troglodytes</i> | Chimpanzee | 386 (20) | 289 (10) | 226 (24) | 901 (54) | 5.99 |
| <i>Gorilla gorilla gorilla</i> | Western lowland gorilla | 289 (44) | 257 (28) | 196 (37) | 742 (109) | 14.69 |
| <i>Hylobates klossii</i> | Kloss's gibbon | 45 (6) | 52 (2) | 42 (0) | 139 (8) | 5.76 |
| <i>Simias concolor</i> | Pig-tailed langur | 54 (13) | 57 (16) | 51 (6) | 162 (35) | 21.60 |
| <i>Papio hamadryas</i> | Hamadryas baboon | 72 (27) | 69 (26) | 64 (14) | 205 (67) | 32.68 |
| <i>Macaca fuscata</i> | Japanese macaque | 154 (43) | 143 (36) | 128 (43) | 425 (122) | 28.71 |
| <i>Paranthropus robustus</i> | | 52 (7) | 43 (2) | 43 (5) | 138 (14) | 10.14 |
| <i>Australopithecus africanus</i> | | 49 (13) | 67 (12) | 52 (5) | 168 (30) | 17.86 |
| <i>Homo naledi</i> | | 28 (17) | 19 (7) | 12 (5) | 59 (29) | 49.15 |

Table 2

Mean wear scores for all three permanent molars combined, divided by buccal and lingual sides and by maxilla/mandible. Wear scores were calculated following Scott (1979). Bold figures indicate side with greatest mean wear score.

| Species | Common name | Maxilla | | | Mandible | | |
|-----------------------------------|-------------------------|---------|-------------|------------|-------------|---------|------------|
| | | Buccal | Lingual | Difference | Buccal | Lingual | Difference |
| <i>Pan troglodytes</i> | Chimpanzee | 3.45 | 4.24 | 0.79 | 4.36 | 3.56 | 0.80 |
| <i>Gorilla gorilla gorilla</i> | Western lowland gorilla | 3.44 | 4.43 | 0.99 | 4.35 | 3.43 | 0.92 |
| <i>Hylobates klossii</i> | Kloss's gibbon | 3.47 | 4.89 | 1.42 | 4.51 | 4.08 | 0.43 |
| <i>Simias concolor</i> | Pig-tailed langur | 3.49 | 5.29 | 1.80 | 5.99 | 3.59 | 2.40 |
| <i>Papio hamadryas</i> | Hamadryas baboon | 3.54 | 5.39 | 1.85 | 6.12 | 4.19 | 1.93 |
| <i>Macaca fuscata</i> | Japanese macaque | 4.20 | 5.44 | 1.24 | 6.10 | 5.05 | 1.05 |
| <i>Paranthropus robustus</i> | | 3.72 | 3.91 | 0.19 | 3.64 | 3.28 | 0.36 |
| <i>Australopithecus africanus</i> | | 3.23 | 3.54 | 0.31 | 3.88 | 3.45 | 0.43 |
| <i>Homo naledi</i> | | 3.22 | 3.65 | 0.43 | 3.96 | 3.22 | 0.74 |

buccal and lingual wear, which, particularly for mandibular teeth, approached extant great apes in terms of difference in mean wear scores (Table 2). In contrast, based on differences between lingual and buccal sides, *P. robustus* teeth exhibit the most even wear of all species (Table 2).

Chipping patterns vary among samples; however, there are some similarities, with the surface having the greatest overall molar wear (buccal vs. lingual) exhibiting the fewest chips (Table 3; SOM Fig. S1). In all cercopithecids, the highest prevalence of chipping in the upper dentition occurs on the buccal surface. The opposite is true for the lower dentition, with all cercopithecoid species having the highest prevalence on the lingual surface. In apes, the prevalence of chipping varied among surfaces, with interproximal surfaces also commonly fractured. This pattern is especially evident in hominins, with distal chipping in mandibular molars and mesial chipping in maxillary mo-

lars common. However, in all species studied, functional cusps consistently have a lower prevalence of chipping than non-functional cusps, with *H. naledi* being the only exception. When individuals were split into broad 'old' and 'young' categories based on incisor wear, individuals with more tooth wear show a higher prevalence of chipping, but the same pattern is observed in both groups, with little chipping on functional cusps (Table 4).

4. Discussion and conclusions

Results of this study showed that nonfunctional cusps (i.e., buccal half of upper and lingual half of lower molars) present more chipping than their functional counterparts. This does not seem to be affected by tooth wear or age, with similar patterns observed when species are split into two groups, one containing individuals with minimal tooth

Table 3

Percentage of chipped teeth split by crown position for the molars of extant primates and fossil hominins. Bold figures indicate the surface with the greatest share of chips.

| Species | Common name | Maxilla | | | | Mandible | | | |
|-----------------------------------|-------------------------|--------------|--------|---------|--------------|----------|--------------|--------------|--------------|
| | | Buccal | Distal | Lingual | Mesial | Buccal | Distal | Lingual | Mesial |
| <i>Simias concolor</i> | Pig-tailed langur | 44.44 | 11.11 | 16.67 | 27.78 | 5.88 | 23.53 | 52.94 | 17.65 |
| <i>Papio hamadryas</i> | Hamadryas baboon | 65.91 | 9.09 | 4.55 | 20.45 | 5.00 | 25.00 | 60.00 | 10.00 |
| <i>Macaca fuscata</i> | Japanese macaque | 70.77 | 4.62 | 0.00 | 24.62 | 10.71 | 17.86 | 62.50 | 8.93 |
| <i>Pan troglodytes</i> | Chimpanzee | 55.17 | 17.24 | 13.79 | 13.79 | 16.00 | 16.00 | 48.00 | 20.00 |
| <i>Gorilla gorilla gorilla</i> | Western lowland gorilla | 40.28 | 15.28 | 9.72 | 34.72 | 13.51 | 27.03 | 27.03 | 32.43 |
| <i>Hylobates klossii</i> | Kloss's gibbon | 100 | 0.00 | 0.00 | 0.00 | 0.00 | 50.00 | 16.67 | 33.33 |
| <i>Paranthropus robustus</i> | | 50.00 | 0.00 | 0.00 | 50.00 | 9.09 | 45.45 | 18.18 | 27.27 |
| <i>Australopithecus africanus</i> | | 50.00 | 16.67 | 16.67 | 16.67 | 9.52 | 42.86 | 23.81 | 23.81 |
| <i>Homo naledi</i> | | 30.77 | 23.08 | 0.00 | 46.15 | 15.38 | 69.23 | 7.69 | 7.69 |

Table 4

Chipping position and prevalence for three primate species, with individuals split roughly in half based on severity of incisor tooth wear (upper central incisor wear score: 'young': ≤5; 'old': ≥6; Smith, 1984). Bold figures indicates surface with most chips.

| Species | Common name | Mean wear | Chipping rate | Maxilla | | | | Mandible | | | |
|--------------------------------|-------------------------|---------------------|----------------|--------------|--------|---------|--------------|----------|--------|--------------|--------------|
| | | | | Buccal | Distal | Lingual | Mesial | Buccal | Distal | Lingual | Mesial |
| Younger individuals | | | | | | | | | | | |
| <i>Pan troglodytes</i> | Chimpanzee | 3.00 (SD = 1.01) | 4.21 (18/428) | 37.50 | 12.50 | 25.00 | 25.00 | 30.00 | 0.00 | 50.00 | 20.00 |
| <i>Gorilla gorilla gorilla</i> | Western lowland gorilla | 2.67 (SD = 1.17) | 10.71 (27/252) | 58.82 | 0.00 | 5.88 | 35.29 | 20.00 | 10.00 | 40.00 | 30.00 |
| <i>Macaca fuscata</i> | Japanese macaque | 3.88 (SD = 1.82) | 12.03 (19/158) | 33.33 | 0.00 | 0.00 | 66.67 | 15.38 | 38.46 | 46.15 | 0.00 |
| Older individuals | | | | | | | | | | | |
| <i>Pan troglodytes</i> | Chimpanzee | 5.21 (SD = 1.93) | 10.06 (36/358) | 61.90 | 19.05 | 9.52 | 9.52 | 6.67 | 26.67 | 46.67 | 20.00 |
| <i>Gorilla gorilla gorilla</i> | Western lowland gorilla | 5.51 (SD = 2.16) | 20.94 (40/191) | 34.62 | 23.08 | 19.23 | 23.08 | 14.29 | 21.43 | 21.43 | 42.86 |
| <i>Macaca fuscata</i> | Japanese macaque | 7.39 (SD = 1.92) | 42.14 (67/159) | 70.73 | 4.88 | 0.00 | 24.39 | 3.70 | 18.52 | 66.67 | 11.11 |

wear and the other with more advanced wear. The results therefore support human clinical evidence that nonfunctional cusps are more susceptible to fracture (Cavel et al., 1985; Eakle et al., 1986) and suggest this is likely a broader primate characteristic.

There are a variety of explanations why functional cusps have the most overall occlusal wear, yet less chipping. Four possibilities are: (1) chips form relatively uniformly across the crown, but those on the most worn surfaces are removed faster; (2) the masticatory cycle creates variation in stress loads, leading to different parts of the crown being disproportionately affected by shearing and/or crushing; (3) differences in enamel/dental properties between cusps/locations affect the likelihood of fractures/wear forming in alternate parts of the crown (e.g., enamel prism orientation; enamel structure and mechanical properties); and (4) different types of contact (e.g., occluding tooth, dietary items or environmental grit) occur more commonly on certain surfaces, leading to more wear/chips in these locations.

Wear of chips after formation is unlikely to have influenced the results, considering that differences in chipping prevalence remain consistent even in minimally worn teeth (Table 4). Therefore explanations 2, 3, and 4 could explain why functional cusps are less chipped. It has been argued previously that chipping occurs more commonly on nonfunctional cusps in humans because they are less protected (e.g., thinner, less rounded and 'weaker' enamel) than functional cusps (Khera et al., 1990). Because these same enamel side differences are a common feature in primates (Ulhaas et al., 1999), additional protection for functional cusps may help explain the lower levels of chipping in these positions. However, a recent study suggests fracture resistance may be maintained between functional and nonfunctional cusps, despite differences in enamel thickness, through changes in the dentin horn angle (Chai, 2020).

If fracture resistance is truly uniform across molar crowns, then masticatory differences might explain the chipping patterns, with nonfunctional cusps potentially subjected to different forces (Schwartz, 2000). There is evidence to support this hypothesis, at least in part. For example, Dejak et al. (2003) found that the nonfunctional cusps of lower human molars have an unfavorable distribution of stresses when certain items are masticated, which they suggest may explain why these cusps are more susceptible to fracture. There is also variation in forces across occlusal surfaces based on different stages of mastication, which again varies depending on the foods consumed (Menegaz et al., 2015; Vinyard et al., 2008; Wall et al., 2006).

It may therefore be important to consider how different items interact with a tooth during mastication. Tooth to tooth contact leads to more wear on specific parts of the occlusal surface, i.e., contact wear facets; however, contact with certain dietary and nondietary objects such as grit or seeds may affect different locations (Janis, 1984; Koolstra et al., 1988). Similarly, mastication of foods with different mechanical properties, e.g., variation in hardness and toughness, alters mandible movement and timing of the masticatory cycle (Grimoud and Gibbon, 2017; Reed and Ross, 2010); this alteration likely affects which surfaces are subjected to the highest loads and, thus, be potentially more prone to fracture. Axial contacts of hard items with teeth can lead to enamel fatigue and demineralization, meaning that certain crown regions can become more susceptible to fracture as enamel properties change (Gao et al., 2016; Sanchez-Gonzalez et al., 2020). Further research is needed to tease apart these possible factors, and how they may have influenced the chipping patterns in this study.

Other enamel properties may be important, with differences in hardness (resistance to irreversible deformation), toughness (resistance to fracture), and Young's modulus (resistance to reversible de-

formation) found to vary across crowns (Weidmann et al., 1967; Cuy et al., 2002; Farah et al., 2010; He et al., 2011; Akkus et al., 2017; Zhang et al., 2018). These changes in properties may affect the likelihood of different types of wear and fractures (Lawn et al., 2013; Akkus et al., 2017). Relevant to the present study, mechanical properties have been shown to vary between buccal and lingual molar crown positions in humans (Shen et al., 2020; Cuy et al., 2002), suggesting these differences may affect the fracture susceptibility of different surfaces. How prism orientation interacts with occlusal loads was also shown to influence wear and fractures in different mammal species (Rensberger and Koenigswald, 1980; Spears, 1997; Shimizu et al., 2005; He and Swain 2008). Other enamel structural differences between and within teeth are also important to consider, including differences in decussation, thought to protect enamel against fracture (e.g., Macho and Shimizu, 2009; Bajaj and Arola, 2009; Ungar and Lucas, 2010; Constantino et al., 2011, 2012).

Broader characteristics such as occlusal surface area, mandible shape, root morphology, saliva flow/composition, species size, and properties of the surrounding bone may be important considerations for why chipping occurs more commonly on nonfunctional cusps (Khera et al., 1990; Laird et al., 2020; Hartstone-Rose et al., 2015; Thamadilok et al., 2019). In addition, functional cusps usually occlude into a fossa, potentially allowing additional support during compared with nonfunctional cusps (Cavel, 1985). Various behavioral factors may also influence chipping and wear patterns, with many species having developed specialized ways to minimize damage (Hatt et al., 2019; Hatt et al., 2019; Schulz-Kornas et al., 2019; Nakamichi et al., 1998; Allritz et al., 2013; Ito et al., 2017; Ruben et al., 2019). The present results indicate interspecific behavioral and dietary differences do not affect the overall relationship between nonfunctional cusps and enamel chipping, to suggest a strong phylogenetic (morphological or masticatory) influence. For example, the proportion of hard (e.g., seeds), tough (e.g., leaves) and soft (e.g., some fruit) foods consumed by extant primates in this study varies substantially (Hadi et al., 2012; Scott et al., 2018; Whitten, 1982), yet nonfunctional cusps have several times more chips than their functional counterparts in all cases.

Differences between buccal and lingual cusps in terms of mechanical/physical properties and masticatory forces likely contribute significantly to explaining why nonfunctional cusps are more prone to chipping, while consistently exhibiting less wear. Further research on differences in individual chip characteristics and between-cusp occurrence, along with underlying differences in enamel properties, will provide insight into these differences in fracture susceptibility. The results of this study also highlight that other crown positions are potentially more vulnerable to chipping in certain species (e.g., interproximal regions in apes), requiring additional research on mechanical property and mastication patterns.

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Appendix A. Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2020.102923>.

Uncited references

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